A COMPARATIVE STUDY OF DAILY WATER-INTAKE AMONG CERTAIN TAXONOMIC AND GEOGRAPHIC GROUPS WITHIN THE GENUS PEROMYSCUS

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Introduction

It is a widely accepted generalization that many groups of mammals exhibit differences in water consumption which are conditioned upon the available water supply in their respective environments. Bailey (1923) brings out this fact in a striking manner. He states that certain forms exist in hot, barren areas where there is no open water, no available subterranean water, and no precipitation for periods of months or even years. These animals are present in large numbers and are "found in perfect health and good bodily condition with abundance of internal fluids and secretions." Bailey contrasts this type with such animals as the Eastern gray squirrels which "require water once or twice a day and drink a considerable amount at a time." The same author (1923) describes the food habits of several xerophilous forms, stating that their water supply is obtained from seeds, roots, succulent plants, etc. Babcock (1912) shows that the carbohydrates, proteins and fats of foodstuffs are converted into water which is sufficient for a large share of an animal's vital activities.

Whatever may be the actual source of water supply for xerophilous mammals, the fact remains that they are capable of adjusting their vital economy to a very restricted supply of free water.

Dice (1922), in an effort to explain the different habitat preferences of two species of *Peromyscus*, *P. maniculatus bairdii* and *P. leucopus noveboracensis*, tested their water intake in the laboratory. Neither of these forms is xerophilous. Both are found in Illinois, *P. m. bairdii* being a prairie form while *P. l. noveboracensis* is a forest dweller. Dice found no significant difference in water intake between the two species and concluded that "different water requirements cannot be the factor causing the different habitat limitations" of the forms tested.

While acting as research assistant to Dr. F. B. Sumner during the year 1929–30, under a grant from the Carnegie Institution of Washington, the writer was given the opportunity to investigate further the question of differences in water consumption. The experimental subjects used were representatives of five taxonomic groups of mice within the genus *Peromyscus*. These groups were:

P. maniculatus sonoriensis,
P. maniculatus gambelii,
P. maniculatus rubidus,
P. eremicus eremicus,
P. eremicus fraterculus.

The species *maniculatus* is distributed widely over the North American continent. So ubiquitous is this group that Osgood (1909, p. 17) states that "it is probable that a line, or several lines, could be drawn from Labrador to Alaska, thence to Southern Mexico throughout which not a single square mile is not inhabited by some form of this species." The three subspecies of *maniculatus* with which we are here concerned are distributed as follows. *P. m. sonoriensis* is found in arid and desert regions, chiefly in the southwestern United States. *P. m. gambelii* is found along the California coast, south of San Francisco Bay, in the Great Valley of California and also in central Oregon and Washington, east of the Cascades. *P. m. rubidus* confines itself to the humid coastal region from San Francisco Bay, north to the Columbia River.

P. eremicus, which is placed in a distinct subgenus from *maniculatus*, is much more restricted in its geographic distribution. The various subspecies of *P. eremicus* are confined to arid and semi-arid portions of the southwestern United States and adjoining parts of Northern Mexico (Osgood, 1909, pp. 239–240). *P. e. eremicus* is found exclusively in distinctly arid localities, while *P. e. fraterculus* confines itself to the semi-arid coastal region of California, south of Los Angeles, and of northwestern lower California.

It might be expected, on the basis of their varying climatic environments, that these five subspecies would display interesting differences in water intake. The large stock of *Peromyscus* maintained by Dr. Sumner at the Scripps Institution at La Jolla offered ample material for the present investigation. All five subspecific groups described above were represented by "C_1" stock of known age and parentage.[1] It was a comparatively simple task to measure the individual daily water consumption of a portion of this stock. The details of this procedure will be described later.

The problem to be investigated may be briefly stated as follows:

[1] "C_1" is a term used by Dr. Sumner to designate the first generation born in captivity.

are there significant differences in water intake among the five racial groups of *Peromyscus* discussed above? If so, are the differences specific (between species) or subspecific (among diverse races within a species), and how are these variations related to the environmental and phylogenetic backgrounds of the groups in question?

Materials and Methods

Each animal was kept in an individual stock cage, $16 \times 9\frac{1}{2} \times 9\frac{1}{2}$ inches in dimensions, which was divided into a nest compartment and a food compartment. These two compartments were of equal size and were intercommunicating, the latter having a screen front, the former being closed.

In the food compartment the water-supply contrivance was installed. This apparatus had been devised by Dr. Sumner, previous to the time at which the present investigation was undertaken. It was essentially an inverted rimless test tube, resting in a shallow round aluminum dish, $1\frac{1}{4}$ inches in diameter and 3/16 of an inch deep. The test tube was of 16 cc. capacity, and was graduated in cubic centimeters. A small notch in the edge of the tube allowed air to enter this and water to escape into the dish, as it was depleted by the animal's consumption and by evaporation. The device was set up for use as follows. After the tube was filled, the top was covered by the aluminum dish, and it was then quickly inverted and attached firmly by a clamp, in such a manner that the edge of the tube just cleared the surface of the aluminum dish. The water level was then brought down to the 0-cc. graduation by removing small quantities with a pipette.

Distilled water was used. In order to rule out variations in water-intake referable to changes in kind of food, the modified McCollum diet used by Slonaker (1925) was employed. This consisted of the following proportions by weight.

Ground whole wheat	3375
Whole milk powder	500
Casein	750
Sodium chloride	50
Calcium carbonate	75
Sifted ground alfalfa	150
Unsalted butter	250

No green food was given. It may be noted here that under Dr. Sumner's method of caring for the mice they are given no free water. The animals' moisture requirements are met by giving cactus and lettuce, as well as a mixture of alfalfa meal and wheat germ, moistened with milk and cod-liver oil. In a state of nature it seems likely that

Peromyscus, throughout much of its range, does not have access to free water. Therefore it appears that satisfying moisture requirements by drinking free water was a unique experience for the animals tested.

During the entire period of the experiments, the temperature in the experimental room varied from 21° to 24° C., the mean lying between 22° C. and 23° C. Relative humidity was much more variable, the weekly means varied from 40 per cent to 83 per cent. The mean for the entire period was 62 per cent. The maximum variation in humidity during any one experiment was from 30 per cent to 70 per cent, with the mean about 50 per cent. This range during an experiment was exceptional, the normal range being through about 20 degrees. It is obvious that the only strictly fair comparisons are between animals which were tested simultaneously.

The daily water intake of each individual was recorded for a period varying from two to three weeks. During the experimental period, each mouse was transferred from one cage to another in rotation every second day. This procedure was intended to eliminate variations due to the set-up of the water-supply devices.

Four different racial comparisons were made as follows:

(*a*) between *P. m. sonoriensis* and *P. e. eremicus*, involving 55 individuals.

(*b*) between *P. m. gambelii* and *P. e. fraterculus*, involving 57 individuals.

(*c*) between *P. m. rubidus* and *P. m. sonoriensis*, involving 48 individuals.

(*d*) between *P. e. eremicus* and *P. e. fraterculus*, involving 41 individuals.

Four individuals of each of the two races under comparison were usually used in a single experiment. These eight mice were as nearly comparable as possible, in respect to age, and the two sexes were usually equally represented.

I shall use the term "experiment" in referring to each of these comparative tests referred to in the preceding paragraph. Within an experiment, the individuals belonging to a single race, such as *P. e. eremicus* or *P. m. sonoriensis* will be referred to as a "race group." The term "series" will apply to the combined experiments which comprise one of the four racial comparisons: *sonoriensis-eremicus*, *gambelii-fraterculus*, *rubidus-sonoriensis* and *eremicus-fraterculus*.

As stated above, the daily water-intake of an individual was recorded for the duration of the experiment. At the end of the experimental period, the mean daily water-intake for each individual in the experiment was computed, and this value was divided by the weight of the individual in grams. This gives the mean daily water intake in terms of body weight.[2] The weight of each individual was determined to tenths of a gram at the beginning of each experiment. All the figures for water-intake found in Table I are given in terms of cubic centimeters per day per gram.

In each experiment the mean of these individual values for intake per day per gram was determined for each race group. All comparisons between the two races in a series are based upon the difference between the race-group means within an experiment, these differences being weighted by employing the following formula (Sumner, 1915):

$$M_{dif} = \frac{\sum(m - m')(n\,n')}{\sum(n\,n')},$$

in which m and m' are the two corresponding race-group means within an experiment and n and n' are the numbers of individuals upon which the race-group means are based. The value for M_{dif} is the difference in water intake between the two races under comparison in a series.

The probabilities of the racial differences for a series were computed by the method of McEwen (1929) which is based upon "Student's" Probability Integral. The standard deviations from both race-group means within an experiment are obtained. Then the square root of the sum of the squares of these standard deviations is extracted. The difference between the two race-group means is now divided by this standard deviation. The probability corresponding to this value, on the basis of the number of individuals in each race-group, is then found in McEwen's table. This probability value, P, is subtracted from 1.00, giving the probability that the difference is due entirely to chance. The probability that a racial difference within an entire series is due to chance is obtained by multiplying together the values for 1.00 minus P for each race-group difference. This cumulative value I shall refer to as the "series probability."

[2] The standard of cubic centimeters per day per gram was adopted, in spite of the interesting results reported by Richter and Brailey (1929), who studied the water intake of a group of white rats from the age of 30 days to 160 days. These workers found that increase in water intake with age was closely correlated with increase in body surface, but much less closely with increase in body weight. They state further that daily water intake per unit of surface area was found to be practically a constant value at all ages. An attempt was made, in connection with the present investigation, to calculate water intake in relation to surface, and compare the standard of intake referred to surface with intake referred to weight. The results indicated that any differences depending on race were as clearly demonstrated by the use of the body weight standard as by that of body surface. In no case did the water intake per unit of surface approach a constant value as Richter and Brailey found. In view of these facts it was thought justifiable to neglect the intake-surface relationship and use the standard of cubic centimeters per gram of body weight.

TABLE I

		Sonoriensis				*Eremicus*						
	Exper.	No. Indi-viduals	Mean Daily Water Intake *cc's/gram*	Extremes	σ	No. Indi-viduals	Mean Daily Water Intake *cc's/gram*	Extremes	σ	Differ-ence between Means $M_s - M_e$	$1-P$	
Series *A*	1	4	.268	.183–.325	.055	4	.162	.133–.192	.021	.106	.0263	Weighted mean, *sonoriensis*, 0.174
	2	4	.309	.180–.603	.169	4	.139	.114–.162	.017	.170	.0908	" " *eremicus*, 0.124
	3	8	.128	.100–.176	.035	6	.124	.108–.171	.021	.004	.4072	" difference, $M_s - M_e$, +0.037
	4	8	.114	.071–.189	.040	8	.108	.092–.155	.018	.006	.3622	Cumulative value, $1-P$, 0.000017
	5	4	.159	.130–.217	.034	5	.107	.087–.165	.029	.052	.0509	
		Gambelii				*Fraterculus*				$M_g - M_f$		
Series *B*	1	4	.116	.061–.171	.047	4	.078	.046–.109	.022	.038	.1404	Weighted mean, *gambelii*, 0.160
	2	4	.131	.101–.195	.037	4	.098	.071–.141	.026	.033	.1482	" " *fraterculus*, 0.117
	3	4	.185	.164–.208	.017	4	.153	.114–.210	.035	.032	.1257	" difference, $M_g - M_f$, +0.044
	4	4	.145	.126–.160	.013	4	.143	.113–.178	.029	.002	.4622	Cumulative value, $1-P$, 0.0000008
	5	8	.175	.106–.274	.046	8	.118	.082–.197	.033	.057	.0166	
	6	5	.186	.133–.294	.059	4	.109	.101–.127	.010	.077	.0425	
		Rubidus				*Sonoriensis*				$M_r - M_s$		
Series *C*	1	4	.237	.161–.358	.077	4	.372	.155–.534	.182	−.135	.1519	Weighted mean, *rubidus*, 0.200
	2	4	.176	.140–.210	.025	4	.186	.110–.256	.040	−.010	.3703	" " *sonoriensis*, 0.206
	3	4	.190	.157–.222	.023	4	.174	.164–.184	.007	.016	.1683	" difference, $M_r - M_s$, −0.004
	4	4	.187	.169–.211	.015	4	.161	.146–.181	.013	.026	.0469	
	5	8	.205	.145–.283	.044	8	.172	.112–.290	.069	.033	.1625	
		Fraterculus				*Eremicus*				$M_f - M_e$		
Series *D*	1	4	.067	.041–.089	.017	4	.084	.051–.137	.032	−.017	.2383	Weighted mean, *fraterculus*, 0.117
	2	5	.164	.097–.223	.051	3	.136	.118–.148	.012	.028	.2175	" " *eremicus*, 0.107
	3	8	.118	.082–.197	.033	8	.108	.092–.155	.018	.010	.2504	" difference, $M_f - M_e$, +0.007
	4	4	.109	.101–.127	.010	5	.107	.087–.165	.029	.002	.4591	

Results

The results (Table I, Figs. 1, 2, 3) show that, in the *sonoriensis-eremicus* series, *sonoriensis* has a higher water intake than *eremicus;* in the *gambelii-fraterculus* series, *gambelii* surpasses *fraterculus.* If the relative magnitude of these differences within the series A and B are not immediately apparent to the reader, let us note that the weighted difference for the series A, 0.037 cc. per day per gram, is 30 per cent of the weighted mean for *eremicus,* and 21 per cent of the weighted

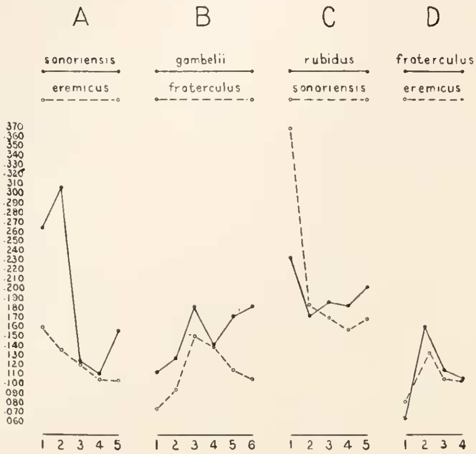
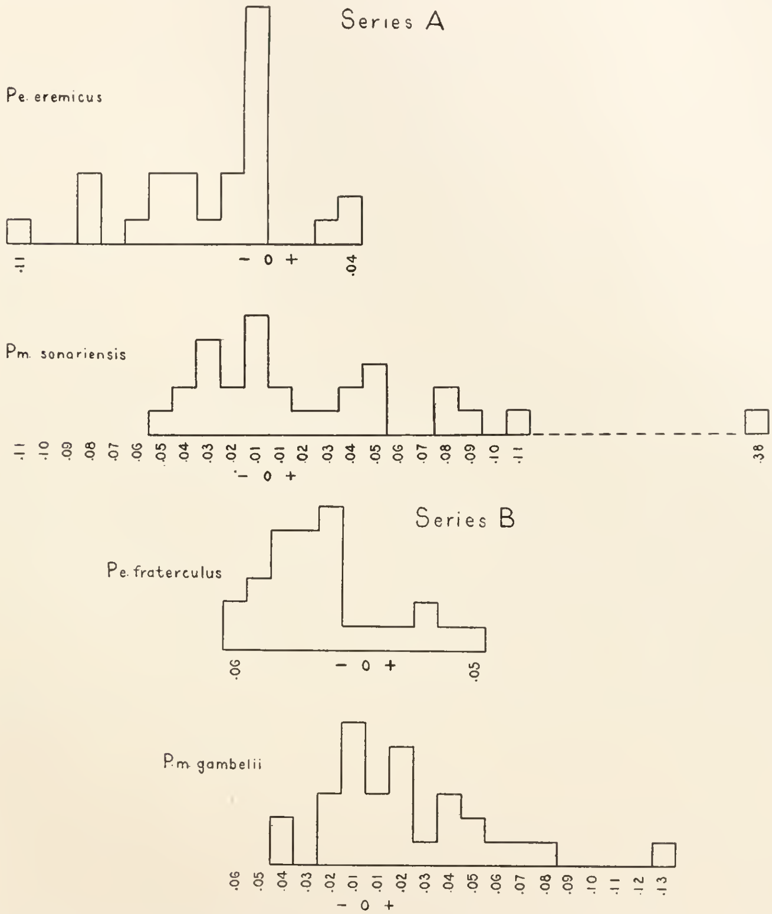


Fig. 1. Graphic representation of the mean value for daily water intake for each experiment in series A, B, C and D. Ordinates indicate water consumption in cubic centimeters per gram per day. Abscissae indicate the series and their component experiments.

mean for *sonoriensis.* Likewise, in series B, the weighted difference, 0.044 cc. per day per gram, is 27 per cent of the weighted mean for *gambelii* and 38 per cent of the weighted mean for *fraterculus.* It will be seen from the table that in none of the component experiments in the series A and B, is the direction of the differences reversed. That is to say, *sonoriensis* is consistently ahead of *eremicus,* and *gambelii* is likewise ahead of *fraterculus* in all cases.

The series probability for series A is 0.000017 and for series B is 0.0000008. This means that in the former series there are 1.7 chances in a hundred thousand that the difference is due to chance, and in the latter series, there is less than one chance in a million that the difference is due to chance. We are therefore forced to the conclusion that the differences obtained in these two series are significant ones.

Combining series A and B, we have an interesting specific comparison, between *Peromyscus maniculatus* (*sonoriensis* and *gambelii*) and *P. eremicus* (*eremicus* and *fraterculus*). The former gives a weighted mean value of 0.167, the latter a weighted mean value of 0.120, the weighted difference being 0.040.



Figs. 2 and 3. Frequency distributions, based upon the deviation (+ or −) of each individual from the mean value (daily water in cc./grams) of the total population of the experiment to which it belonged. In computing this mean value, the two races in each experiment were thrown together and treated as a single population. Values to the right of the zero line represent positive deviations, while those to the left are negative deviations.

Figure 2 is for series *A* and Fig. 3 is for series *B*.

In series *C* and *D* we find, on the other hand, that the weighted differences between the races concerned are very small. The weighted difference in series *C* shows that *rubidus* is 0.006 cc./gram/day ahead of *sonoriensis*. This difference is but 3 per cent of the weighted means for *rubidus* and for *sonoriensis*. In series *D*, *fraterculus* is 0.007 cc./gram/day ahead of *eremicus*. This weighted difference is about 7 per cent of the weighted mean value for *eremicus* as well as of that for *fraterculus*.

In these two series, likewise, we do not find the same consistency in the direction of the differences as was the case in series *A* and *B*. For instance, in series *C*, in three experiments, *rubidus* is ahead of *sonoriensis*, while in two, *sonoriensis* is ahead of *rubidus*. In series *D*, *fraterculus* is ahead of *eremicus* in three experiments, while in the fourth the direction of the difference is reversed.

The small differences within the two series *C* and *D* and the fact that the component experiments display no constancy in the direction of their differences, lead us to the conclusion that we have demonstrated no significant differences in water intake between *P. m. rubidus* and *P. m. sonoriensis*, nor between *P. e. eremicus* and *P. e. fraterculus*.

The reader will perhaps note that the weighted mean water-intake value for *P. m. rubidus* in series *C* is above that for *P. m. sonoriensis* in series *A*. Also, the *P. m. sonoriensis* value in series *A* is above the *P. m. gambelii* value in series *B*. These differences are not considered valid, inasmuch as they are not based upon comparisons between races which were made at the same time, with animals of comparable age, under the same conditions of temperature and humidity. It is entirely conceivable, had all the possible combinations been tested, that other interesting differences might have been brought out. The particular four comparisons were selected as being of especial interest from the viewpoint of the relation between water intake and the environmental and racial backgrounds of the groups concerned.

In the table will be found under "Extremes," the low and high individual values within each racial group, for each experiment. These low and high values, along with the standard deviations, will give the reader some idea of the high degree of individual variability which is displayed by this material. In this connection see also Figs. 2 and 3. These histograms represent the differences in water-intake in terms of the deviation (+ or −) of each individual from the mean for the experiment to which it belongs. It is obvious that the race which has the lower water intake will display predominately minus deviations and that the race with the higher intake will show predominately plus deviations. This predominance of one sign or the other may be manifested either in the greater frequency or the greater magnitude of the deviations in a given direction, or in both respects.

Discussion

We have seen that in our experiments there are significant differences in water intake within the racial groups which have been the subjects of our experimental comparisons. The differences found are between species, representatives of *P. maniculatus* and *P. eremicus*, and not within a species, either *maniculatus* or *eremicus*.

It is also clear that, since the experimental data are based almost exclusively upon material which was born and reared in captivity, under environmental conditions which were identical for the two species under comparison in any single experiment, these differences in water intake are inherited ones.

A rational explanation of the above facts must involve, not only a consideration of the environments of the parent stocks of the experimental material, but some speculation concerning their phylogenetic backgrounds.

Our experimental data point to the probability that *P. m. gambelii* has a higher water intake than *P. e. fraterculus*. While the greater part of the geographic distribution of *gambelii* embraces a region in which more humid climatic conditions prevail than in the range of *fraterculus*, the range of the former does to a certain degree overlap that of the latter. The two forms occur together in the coastal belt of California, south of Los Angeles, and in the northern coastal region of Lower California. It is from this overlapping region that the parent stocks of experimental material for both races were secured.

It has been indicated in our experiments that *P. m. sonoriensis* has a higher water intake than *P. e. eremicus*. In considering the geographic distribution of these two races, we see that their ranges overlap to a certain degree and that where their ranges do not overlap, similar climatic conditions prevail.

Here we have two cases (*gambelii-fraterculus*, *eremicus-sonoriensis*), in which two forms belonging to separate species of the genus *Peromyscus* are found in a state of nature living under similar climatic conditions, but as tested in the laboratory, show very definite differences in water intake.

It seems evident then that we must search farther than adaptation to the general climatic environment of a region for an explanation of the differences in water intake which we have found. Perhaps we may find the solution in a consideration of the racial backgrounds of the groups with which we are concerned. From the geographic distribution of the two species of *Peromyscus*, *maniculatus* and *eremicus*, we may deduce much concerning their probable evolutionary histories. The reader is referred to Osgood's (1909) maps of geographic distribution for *P. maniculatus* and for *P. eremicus*. It will again be noted, as mentioned in the introduction, that the species *maniculatus* has a very widespread distribution. Although it is fairly well represented in the arid and semi-arid southwest, perhaps eight or nine-tenths of the geographic range of this very ubiquitous species is in more humid regions. The species *eremicus*, on the other hand, has a much more limited distribution, being essentially a southwestern form, confined to arid regions of southwestern United States and nearby portions of Mexico.

May we not frame a somewhat speculative explanation of the difference in water intake between *maniculatus* and *eremicus*, on the basis of their probable racial histories deduced from their geographic distributions?

We may suppose that the stem form from which the numerous sub-species of *P. maniculatus* were differentiated had its origin in a relatively humid environment. This assumption is a safe one, since desert habitats for *maniculatus* are exceptional, perhaps ten per cent of its total geographic distribution. After a lapse of time, the group extended its geographic range from its point of origin, some forms migrating to more arid localities. These forms became slowly adapted to the environmental conditions encountered there, but may have retained to some extent the ancestral modes of life.

A similar line of thought may be applicable to the case of *P. eremicus*. We may suppose that the *eremicus* stem-form had its origin in an arid locality and gradually extended its range. Some groups became adapted to a certain extent to less arid climatic conditions but retained many of the characteristics of the ancestral type.

There are observations by various workers concerning the habitat preferences of certain races of *Peromyscus*, which are very interesting in connection with the foregoing discussion of racial history, and also with the experimental results which I have obtained. Dr. F. B. Sumner states it as a matter of practical field experience that when trapping for *Peromyscus* in a given locality, *P. maniculatus* is found more typically in relatively moister habitats, while *P. eremicus* prefers more arid situations. For instance, in certain arid regions, this worker finds that *P. m. sonoriensis* is taken in large numbers along flood plains of rivers and other low-lying ground, where relatively few *P. e. eremicus* are caught. When the trap-line is run up on the arid banks and barren slopes, even a few hundred yards away, *eremicus* may be obtained in large numbers, while *sonoriensis* is scarce. There is a similar relationship between *P. m. gambelii* and *P. e. fraterculus* in the coastal region of Southern California. *Gambelii* is taken in large numbers in grassy valleys and the bottoms of canyons, while *fraterculus* is more often found in abundance on the dry hillsides.

Grinnell (1914) in his "Account of Mammals and Birds of the Lower Colorado Valley" states that *P. m. sonoriensis* is an "abundant inhabitant of bottom lands everywhere" and that "this *Peromyscus* [*P. m. sonoriensis*] has appropriated the river bottom, which, in turn, is tabooed by the two desert species of the region, *eremicus* and [*P. crinitus*] *stephensi*." And of *P. e. eremicus*, the same author says "yet our trapping showed distinct associational preferences. The overflow bottom is evidently rarely invaded, there being but slight overlapping of the habitat of *P. maniculatus sonoriensis*."

It appears then, that *P. e. eremicus*, even though it may occur under the same climatic conditions as *P. m. sonoriensis*, is influenced by its racial background in such a manner as to display a predisposition to a lower water intake than *sonoriensis*, and to seek an immediate habitat which is compatible with this tendency. Likewise, *P. e. fraterculus*, although its geographic range overlaps to a certain extent that of *gambelii*, consumes less water than the latter, because of an inherited predisposition to a more limited water intake. *Fraterculus* and *gambelii* show habitat preferences in accordance with this physiological character.

In view of the fact that no differences in water intake were demonstrated between *P. m. rubidus* and *P. m. sonoriensis*, we may suppose, pending further investigation, that *sonoriensis* has not yet diverged sufficiently from forms such as *rubidus* to display a difference in water intake sufficient to be demonstrated by the somewhat crude methods employed in this investigation. Likewise, since no water-intake difference could be proved between *P. e. eremicus* and *P. e. fraterculus*, it would appear that *fraterculus* is not at present far enough removed from *eremicus* to show a significant difference in water consumption.

Summary

1. Five subspecific groups of *Peromyscus*, representative of the two species, *maniculatus* and *eremicus*, have been tested in the laboratory to determine whether racial differences in water intake exist.

2. Significant differences were found between *P. m. sonoriensis* and *P. e. eremicus*, as well as between *P. m. gambelii* and *P. e. fraterculus*. No significant differences between *P. m. rubidus* and *P. m. sonoriensis*, nor between *P. e. eremicus* and *P. e. fraterculus*, were demonstrated.

3. It is seen that, in these experiments, the only demonstrable differences in water intake are between the two species, *P. maniculatus* and *P. eremicus*, and not within either species. These specific differ-

ences in water intake are interestingly correlated with the geographic and ecological distributions of the two species.

4. Since the experimental data are based almost exclusively upon cage-bred stock, reared in a common environment, these differences appear to be hereditary.

5. Adequate statistical treatment, using McEwen's method, based upon "Student's" Probability Integral, indicates that these differences in water intake are real ones and not due to chance.

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